

FLOWER PRODUCTION IN THE LEMNACEAE.*

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The general evolutionary movement in the Lemnaceae or duckweeds apparently has been from frequent flower production to rare flower production to a total loss of the ability to produce flowers. From the original ancestral forms, which perhaps depended entirely upon seed production for propagation, have evolved these minute plants which now are propagated almost entirely or solely by vegetative methods. The family consists of four genera and about 26 known species.

In *Spirodela* flowers are very rarely produced. Wiggers, 1780 (36), records the first discovery of *Spirodela polyrhiza* (L.) Schleiden in flower by Grauer, a young botanical student. Flowers of this species were first discovered in the United States at Staten Island, N. Y., by Leggett, 1870 (22a). Others who have recorded flowering are Willdenow, 1805 (37), Schleiden in Germany, 1839 (30), Griffith in India, 1851 (14a), Nees von Esenbeck as recorded by Hoffman, 1840 (17) and Ludwig, 1909 (24b), Gillman, Belle Isle, Detroit River, Michigan, 1871 (13b) and 1881 (13c), Rostowzew, 1901 (28a) and Saeger in Missouri, 1929 (29). *Spirodela punctata* (Meyer) Thomp., collected by the Capt. Wilkes Expedition in Terra del Fuego, South America in 1839, was described as flowering by Thompson, 1898 (31). Flowers of *Spirodela oligorhiza* Kurz were described by Kurz, 1865 (21). A fourth species found in Australia, *Spirodela pusilla* Hegelm, apparently flowers more commonly than any species of the genus, Hegelmaier, 1895 (15a).

The flowers and even matured fruits of *Lemna* have been found occasionally in all species and many have been studied in detail. Micheli 1729 (25) first records flowers of *Lemna gibba* L. Ehrhart, 1779 (9), Wolff, 1801 (39), Palisot, 1816 (26), Wilson, 1830 (38), Brongniart, 1833 (4), Richard, 1833 (27), Schleiden, 1839 (30), Dalglish, 1926 (16), and a number of other authors have recorded flowers of this species. *Lemna trisulca* L. apparently was first reported in flower by Wolff,

*Papers from the Department of Botany, Ohio State University, No. 295.

1801 (39) and had since been found flowering under natural conditions by a number of authors. *Lemna perpusilla* Torrey was first described and also found in flower at Staten Island, N. Y., by Torrey, 1843 (32), and again by Leggett, 1870 (22a), and studied in detail by Blodgett, 1914 (2a) and 1923 (2b).

Lemna minor L. was the only duckweed known in flower to Linnaeus, 1763 (23). This species undoubtedly blooms more frequently than any other as it has been reported in the flowering condition by no less than thirty authors. Some flowering plants were observed by the writer during the summers of 1928, 1929, 1930 and 1931. In May, June, July, August and September of the growth period of 1930, flowering plants were found in abundance in many widely separated localities of Ohio. Wolff, 1801 (39), Vuyck, 1895 (34a), Kalberlah, 1895 (19), Rostowzew, 1901 (28a) and 1905 (28b) and Goebel, 1921 (14) gave detailed descriptions of the reproductive structures. Caldwell, 1899 (5), made a complete life history study of the species.

Flowers in the genus *Wolffia* are extremely rare, difficult to detect because of their small size, and have never been found for two species, *W. microscopia* Griff. and *W. cylindracea* Welw. *W. papulifera* Thomp., a species known only from Missouri and bordering states and described by Thompson in 1897 (see 1898, 31), was unknown in flower until discovered by Saeger in 1927 and 1928 (see 1929, 29). Flowers of *W. brasiliensis* Weddell were first described by Weddell, 1849 (35), *W. arrhiza* (L) Wimmer by Franchet, 1864 (12), *W. hyalina* (Delile) Hegelm., by Hegelmaier in 1865 (15), *W. columbiana* Karsten by Karsten in 1865 (20) and by Austin, 1870 (1), *W. repanda* Hegelm. by Hegelmaier in 1868 (15b), *W. Wetwitschii* Hegelm. by Hegelmaier in 1868 (15b), and *W. punctata* Griseb. mentioned or described vaguely by several writers. Additional known occurrences of flowering in the genus are certainly rare as the writer was able to secure very few other definite records in making an exhaustive survey of the literature.

In the genus *Wolffiella* reproduction is entirely by the vegetative method as none of the four known species (*W. floridana* (J. D. Smith) Thomp., *W. gladiata* Hegelm., *W. oblonga* (Ph) Hegelm., and *W. lingulata*) have ever been observed in the flowering condition. The ability to produce

flowers apparently has been so completely lost that probably they are never produced by plants in nature. In *Wolffiella floridana*, at least, it is even doubtful as to whether the flowering potentiality could be made to find expression as the result of favorable physiological conditions.

It has been noted by the writer a number of times and by others (Gillman, 13a, Leggett, 22b, and Saeger, 29), that bodies of water having one flowering species are likely to also have a second or a third. Apparently then, even in nature, unusual combinations of either chemical or non-chemical environmental factors may develop locally in a small body of stagnant water, and make possible the expression of the flowering potentiality which still exists in *Spirodela*, *Lemna*, *Wolffia* and perhaps in *Wolffiella* as well. These necessary combinations do not commonly occur, but certain species, such as *Lemna minor* and to a lesser extent *L. trisulca*, are much more responsive to these effects than the other members of the family.

During the drowth period, or the months of May to September inclusive, of the summer of 1930, dozens of small bodies of water supporting duckweed populations dried up completely or were greatly decreased in size. In a number of these habitats, the water supply failed for what, certainly, was the first time within recent history or perhaps since the settlement of this state. All aquatic vegetation was subjected to most unusual growth conditions. In many shallow pools, duckweeds of several species were left stranded on mud flats with a steady but limited water supply. In other cases, the lowering waters left tangled masses of *Lemna* or *Spirodela* draped about stems of *Cephalanthus occidentalis* or other aquatic shrubs. If the plant mass dipped into the water beneath, a limited but sufficient water supply for life was maintained. During this period some field work was done in each one of the 88 counties of Ohio. Under these conditions two species were found in flower in a number of widely separated localities of Ohio from May 20 to Sept. 6, 1930.

Lemna minor and *L. trisulca* were found in flower at Suffield Bog (Portage Co.), Venice (Erie Co.), Buckeye Lake (Perry Co.), Baumgardner's Pond (Franklin Co.), and Calamus Pond (near Circleville; Pickaway County). In addition *L. minor* alone was found in flower at Jasper (Pike Co.), Athens (Athens Co.), Fredericktown (Knox Co.), Indian Lake (Logan Co.) and

Tamarack Ditch (Williams Co.). No other species were found blooming although large areas of plants growing in more than 180 localities of the state were studied, all of our 7 Ohio species being represented.

In 1928, 1929 and 1931, a similar survey revealed only a few scattered instances of flowering, and then flowering plants were always decidedly uncommon. As to what environmental factors accompanying the drouth, were responsible for the unusual flower production in 1931, can only be a matter of speculation. In many instances, observations suggested that altered mineral content of the water medium, increased water and air temperatures, or light effects might be of most importance.

Flowering plants, without exception, were never found in shaded areas, even though abundant flowering material might be found in better illuminated areas a few feet distant. In most cases, flowers were most abundant in areas most exposed to sunlight. Correlated with this was the observation that flowering plants were invariably found abundantly only in water areas of unusually high temperatures and were absent in colder portions. In addition, since *Lemna minor* flowered in only about 8% of all of the localities visited, and since the visible environmental characteristics of many localities appeared to be almost the same, it was suggested that the chemical nature or mineral content of the water medium might inhibit or be an important factor in promoting flower production.

In *Lemna minor*, flowering plants observed were usually somewhat above average size for the species, commonly light green in color and with long roots, and invariably quite cavernous. In *Lemna trisulca*, the extremely modified flowering plants of the species were very light green in color, were quite cavernous and were produced by buoyant plants of medium size having relatively short internodes. With both species, flowering plants produced were similar in general appearance to those previously produced by experimental methods as described below.

In all available literature concerning the Lemnaceae, the writer has found but one reference concerning the production of flowering plants outside of their natural environment. Saeger, 1929 (29), found that cultures of *Lemna minor* growing in dilute mineral solutions (Knop's), sometimes produced

flowers. Other species of *Lemna* grown failed to produce flowers. No references to any experimental attempts to induce flower production, have been found. Therefore, it seemed desirable to make a test of all possible treatments and environmental controls which might alter physiological processes and induce or lead to control of flower production. This paper is largely a revision of a previous paper written in May, 1929, summarizing a series of experiments conducted from Nov. 1928 to May 1929. The writer wishes to acknowledge his indebtedness to Dr. E. N. Transeau and Dr. B. S. Meyer, for their many valuable suggestions and criticisms in this research and to Dr. Robert B. Gordon and Mr. W. C. Camp for their assistance in taking the photographs and microphotographs of flowering plants.

Previous experimental work had demonstrated that there were remarkable differences between our 7 Ohio Lemnaceae species in their reactions to various environmental conditions. This suggested that each species might require its own particular treatment or that those influences which had favored flower production in other plant families, might not apply to this one. Each species, perhaps, has reached its own particular physiological level in regard to the possible expression of the flowering potentiality. The factors inhibiting flower production, which have come into the systems of some of the species in the evolutionary process, are perhaps so dominant that they may never be overcome, even under artificial conditions. From the above, it will be seen that the problem of inducing flower production is a very complex one. The writer has been successful in producing flowers in four species and one variety of the genus *Lemna* and in one species of the genus *Wolffia* by experimental methods affecting the physiological condition. Flowers were produced in *Lemna trisulca*, *L. cyclostasa*, *L. minor*, *L. minor* var. *purpureus* *L. minima* and *Wolffia columbiana*.

The experiments showed that for flower production the following conditions are necessary:

1. Healthy mature plants making good vegetative growth and with an accumulation of a food reserve.
2. Some environmental influence which will rather suddenly check normal vegetative growth with the possible diversion of the accumulated reserve to flower production.

3. In some species, such as *Lemna trisulca*, which undergo a marked transformation of the vegetative form at the time of blooming, plants should be selected for treatment which are as near as possible in appearance to the flowering form as such transformations do not come about rapidly. Not all growth forms are equally responsive to experimental treatments.

In all of the experimental work with flower production, *Spirodela polyrhiza*, *Lemna trisulca*, *L. minor*, *L. minor* var. *purpureus*, *L. cyclostasa*, *Wolffia columbiana*, *W. punctata* and *W. floridana* were used. Plants were grown in about 4 inches of water in glazed culture jars of 28 sq. in. of water surface area and under greenhouse conditions. In every experiment attempted, lots of 1000 or more plants of each species were used to make it possible to observe any results produced, on large numbers of individuals. In many cases, smaller cultures of 1 to 25 plants of each species were treated similarly and used as checks. The record of the various experiments attempted with the results obtained is as follows:

1. MINERAL SALT DEFICIENCY.—During the experimental work approximately 850,000 plants of all species (about 460,000 of *Lemna minor*) were "starved" by growing in various nutrient solutions known to be deficient in one or more of all of the elements considered essential, in tap water or in various soil-water solutions. The plants became small in size, produced resting forms in many cases and eventually died, but as far as is known, not a single plant produced flowers. The "starvation" process is a gradual checking of vigorous vegetative growth with the loss of any food accumulation or reserve which might favor flower production if present. This method, then, gives no promise of desired results.

2. NUTRIENTS. All of the species were grown in numerous nutrient solutions of varied combinations and concentrations. Many of the unbalanced nutrients produced size reduction or resting forms. Some produced marked modifications of the vegetative form as in *Lemna cyclostasa*. Nutrients with an excess of nitrates or those containing abundant organic matter, usually produced vigorous vegetative growth but without exception, there was no flower production. The following nutrients were also tested: Knop's, Knop-Bottomly, Detmer-Moor, Detmer's, Pfeffer's, Crone's and Shive's. Several others were used in a few instances but no plants grown produced flowers.

3. PHOTOPERIODISM. Several of the species made vigorous growth during the reduced light of the winter months if other environmental factors were satisfactory. Seven species were grown for five months under 24 hour light in various media. All produced somewhat better growth than the controls under natural light but *Spirodela polyrhiza* exhibited a marked tendency to develop excessive pigmentation. This species and the *Wolffias* also produced resting forms freely. When these plants were suddenly changed to shorter light periods, no flower production took place and no other very pronounced modifications occurred. During the winter months, cultures of each species were subjected to 2, 4 and 6 hours of artificial light daily over a three-week period in addition to the normal sunlight period. These cultures made only slightly better growth than the controls under daylight. Flowers were never produced in any of these experiments.

4. LIGHT INTENSITY. Plants of 7 species were subjected to five different light intensities of artificial light for 2, 4, 6, 8 and 10-week periods by various degrees of shading, with marked effects resulting in the vegetative form as in *Spirodela polyrhiza*, but no plants developed flowers.

5. CHEMICAL EFFECTS. Approximately 60 common chemical substances were added in varying quantities to the media in which six species of duckweeds were growing. Results were negative except in one case. Flowers of *Lemna minor* and *L. trisulca* were abundantly produced by treatment with dilute sodium hydroxide. This treatment failed to produce flowers in any of the other species and often failed to produce them in these species when repeated. In each case, a culture solution with a mat of plants of approximately 28 square inches was treated. A small amount of the dilute sodium hydroxide was added to the medium for several days until a few of the plants showed signs of injury. The amount required varied considerably. Then treatments were stopped. Usually from 1% to 10% of the plants were killed, the remainder nearly or entirely stopped vegetative growth and a few of them were thrown into the flowering condition. The first treatments began March 28, 1929 and the first flowers were discovered on April 15, 1929. Some flower production continued up to May 16, 1929. The mediums gradually became less alkaline and the hydrogen ion concentrations of the mediums at the time for the greatest

flower production on April 22, 1929 is shown. No flowers were produced in any of the check cultures. The records for each culture are as follows:

SPECIES AND COLLECTION	FIRST FLOWERS	PERCENT OF PLANTS FLOWERING	P. H. AT TIME OF FLOWERING
1. <i>Lemna minor</i> Coll. at Baumgardner's Pond, Franklin Co., 3-27-29.....	4-15-29	15%	7.6
2. <i>L. minor</i> Coll. at Baumgardner's Pond Bog, 3-27-29..	4-17-29	12%	7.21
3. <i>L. minor</i> Coll. at Cranberry Is., Buckeye Lake, 3-25-29...	4-16-29	26%	7.33
4. Same as No. 2.....	4-17-29	20%	7.43
5. Same as No. 3.....	4-19-29	10%	7.41
6. <i>L. minor</i> Coll. at Westerville, Franklin Co., 3-6-29.....	4-15-29	20%	7.21
7. <i>L. minor</i> from De Land, Fla., 3-1-29.....	4-16-29	5%	7.35
8. <i>L. trisulca</i> Coll. on Cranberry Is., Buckeye Lake, 3-25-29.....	4-19-29	8%	7.16
9. <i>L. trisulca</i> Coll. at Baumgardner's Pond Bog, 3-27-29..	4-23-29	30%	7.21

6. ULTRA-VIOLET RAYS. Flowers of *Lemna minor*, L.m. var. *purpureus*, *L. trisulca* and *L. cyclostasa* were abundantly produced in cultures treated with ultra-violet rays from a mercury quartz vapor lamp. Sixteen earthenware culture jars of approximately 28 square inches of water area each were prepared. To each was added a small amount of rich clay loam soil containing considerable organic matter and then filled with tap water. Each jar was given the following duckweed population. The numbers of each are only approximate: *Spirodela polyrhiza* 75, *Lemna trisulca* 100, *L. minor* 150, L.m. var. *purpureus* *L. cyclostasa* 150, *Wolffia columbiana* 400, *W. punctata* 200 and *W. floridana* 50.

Every other jar of duckweeds was selected as a control and the others were subjected to the ultra-violet treatment. A 110-Volt lamp, at a distance of 30 inches was used. The time

of the treatment of the 8 culture pairs was 8, 16, 27, 39, 51, 63, 75 and 87 minutes respectively. Treatment was given on April 19, 1929 and the first flowers appeared 13 days later on May 2, 1929. Not a single flower was produced in any of the control cultures.

No plants of *Spirodela*, *Wolffia* or *Wolffiella* were thrown into flowering. Vegetative growth of all of the species was almost or completely checked. None of the plants except those of *Spirodela* was visibly affected by the ultra-violet rays. These were usually rather severely burned by the rays in all except those given the 8-minute treatment. The burned plants seemed damaged only on the upper surface. They became heavily pigmented, shriveled and gradually died but were rapidly rejuvenated by the production of vigorous normal plants. All of the *L. cyclostasa* plants producing flowers were small, pale green, decidedly unsymmetrical and with short roots.

The records of each culture are as follows:

	First Flowers Produced	Approximate Percent of Plants Flowering		First Flowers Produced	Approximate Percent of Plants Flowering
1. 8-MINUTE ULTRA- VIOLET TREATMENT			5. 51-MINUTE TREATMENT		
<i>L. minor</i>	5-4-29	15	<i>L. minor</i>	5-5-29	10
<i>L. m. var.</i>			<i>L. m. var.</i>		
<i>purpureus</i>	5-2-29	20	<i>purpureus</i>	5-5-29	30
<i>L. trisulca</i>	5-2-29	10	<i>L. trisulca</i>	5-4-29	5
<i>L. cyclostasa</i>	5-6-29	3	<i>L. cyclostasa</i>	5-8-29	15
2. 16-MINUTE TREATMENT			6. 63-MINUTE TREATMENT		
<i>L. minor</i>	5-3-29	30	<i>L. minor</i>	5-4-29	10
<i>L. m. var.</i>			<i>L. m. var.</i>		
<i>purpureus</i>	5-2-29	25	<i>purpureus</i>	5-5-29	50
<i>L. trisulca</i>	5-2-29	15	<i>L. trisulca</i>	5-5-29	55
<i>L. cyclostasa</i>	5-5-29	2	<i>L. cyclostasa</i>	5-8-29	5
3. 27-MINUTE TREATMENT			7. 75-MINUTE TREATMENT		
<i>L. minor</i>	5-4-29	20	<i>L. minor</i>	5-3-29	5
<i>L. m. var.</i>			<i>L. m. var.</i>		
<i>purpureus</i>	5-4-29	25	<i>purpureus</i>	5-5-29	30
<i>L. trisulca</i>	5-3-29	15	<i>L. trisulca</i>	5-6-29	5
<i>L. cyclostasa</i>	5-5-29	10	<i>L. cyclostasa</i>	5-8-29	10
4. 39-MINUTE TREATMENT			8. 87-MINUTE TREATMENT		
<i>L. minor</i>	5-4-29	15	<i>L. minor</i>	5-6-29	2
<i>L. m. var.</i>			<i>L. m. var.</i>		
<i>purpureus</i>	5-5-29	30	<i>purpureus</i>	5-6-29	10
<i>L. trisulca</i>	5-4-29	15	<i>L. trisulca</i>	5-8-29	3
<i>L. cyclostasa</i>	5-5-29	10	<i>L. cyclostasa</i>	5-7-29	5

ADDITIONAL EXPERIMENTS WITH ULTRA-VIOLET TREATMENTS.

On March 25, 1930, the foregoing experiments with ultra-violet light treatments of duckweed plants were repeated. The same species were used and one other in addition, *Lemna minima* Phillipi, a species not recorded for Ohio. This time the plants were placed 38 centimeters from the light source of the mercury quartz vapor lamp, and by measurement received 86 milliamperes on slit No. 3 or 105 ergs per second per square millimeter of area. Treatments of 3, 5, 10, 15, 20 and 25 minutes were used. No attempt to measure or determine the exact quality of the light used was made but the rays proved to be much more destructive than those used in 1929.

The table below illustrates the amount of visible injury to plants in each case:

	LENGTH OF TREATMENT IN MINUTES					
	3'	5'	10'	15'	20'	25'
<i>Spirodela polyrhiza</i>	Slight effect	Slightly burned	Much burned	Much burned peeled	Very much burned peeled	Very much burned peeled
<i>Lemna minor</i>	No effect	No effect	No effect	Some burned	Burned pale	Epi-dermis peeled
<i>L. minor</i> var. <i>purpureus</i>	No effect	No effect	Slight effect	Some burned	Much burned	Burned and peeled
<i>L. trisulca</i>	No effect	No effect	No effect	No effect	Some browned	Much browned
<i>L. cyclostasa</i>	Slight effect	Slightly browned	Browned	Well browned	Much browned	Very much browned
<i>L. minima</i>	No effect	Slight effect	Slightly browned	Browned	Well browned	Much browned
<i>Wolffia columbiana</i>	No effect	No effect	No effect	Slightly browned	Slightly browned	Burned browned
<i>W. punctata</i>	No effect	Slightly browned	Slightly browned	Browned	Much browned	Browned burned
<i>Wolffiella floridana</i>	No effect	No effect	No effect	Slight effect	Slightly browned	Browned

Plants of *Spirodela* receiving 3 or 5 minute treatments continued growth without any flower production. Plants receiving 10, 15, 20 and 25 minute treatments had most of the cells of the upper parts killed. These plants were quickly replaced by budding of new plants from the treated ones, resulting in stimulated vegetative growth, just opposite to the results desired. It is interesting to note that the submerged species were not so severely effected by the light treatments. In the longer treatments, a number of the plants of each species died. Flower production following treatment was very similar to the results obtained during the 1929 experiments except that the percentage of plants producing flowers was less and also the amount of flower production did not always seem to have any definite relation to the length of light treatment received. As before, not a single flower was produced in the untreated cultures. Two additional species produced flowers in the treated cultures.

Spirodela polyrrhiza, *Wolffia punctata* and *Wolffiella floridana* failed to produce any flowers. In *Lemna minor* and *L. m. var. purpureus*, from 5 to 20% of the plants receiving 10, 15 and 20 minute treatments produced flowers. In *Lemna cyclostasa*, 1 to 3% of the plants receiving the 5, 10 and 15 minute treatments flowered. In *L. minima*, three plants receiving the 10-minute treatment produced imperfectly developed flowers. Two plants of *W. columbiana* receiving the 15-minute treatment flowered, the first flowers known to have been produced by the species except in very rare instances by plants growing under natural conditions. This species is credited with the distinction of being the smallest flowering plant in the world.

SUMMARY.

1. A review is made of the known occurrences and frequency of flower production under natural conditions in the various species of Lemnaceae.
2. A report is given of observations made upon several Ohio species found flowering under natural conditions.
3. A summary is made of a series of experiments in which treatment was made to induce flower production, through the control of various environmental factors.
4. *Lemna minor*, *L. m. var. purpureus*, *L. trisulca*, *L. minima*, *L. cyclostasa* and *Wolffia columbiana* produced flowers following ultra-violet light treatments. The first three named

also produced flowers following chemical treatment with sodium hydroxyde. No flowers were produced by control cultures in either case.

5. A list is presented of the conditions thought necessary for flower production in the family.

6. Photographs and microphotographs of the minute flowers of two species are presented to show the detailed structure of these parts.

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EXPLANATION OF PLATES.

PLATE I.

Vegetative and flowering plants of *Lemna trisulca* L. Ivy-joined or Star Duckweed, produced following experimental treatments.

(a) Vegetative plants shown around the margins of the photograph are of the submerged type, being compact in structure and of about the same density as the water medium. The plants are flat, oblong-lanceolate in shape and connected with long internodes, many generations remaining attached forming tangled masses. This growth form is dark green in color, somewhat unsymmetrical in shape with finely serrate margins and usually an acute apex, does not have developed stomata or papules and produces long roots attached at the nodes. Magnification about 3X.

(b) Flowering, floating plants found attached in groups of 3 or 4, (center of photograph). These floating plants are produced by abscission from the submerged vegetative form. They are much smaller and are convexly curved, have very short internodes, are light green in color and decidedly cavernous, having a density of less than one, and develop stomata, but fail to produce roots. Usually one or two of the floating plants of each group produce flowers. The flowers develop from the node, growing out through the plant body, and are monocious, consisting of two stamens with two pollen sacs in each anther and a single flask-shaped pistil, enclosed in a spathe. The anthers are commonly covered with a drop of clear glandular secretion until the opening of the pollen sac.

PLATE II.

(a) Left. Microphotograph of a single flower of *L. trisulca* L. showing the spathe, the two stamens with two pollen sacs each and the single flask-shaped pistil. Magnification about 100X.

(b) Right. A flower of *L. minor* L. illustrating the same structures. Note the difference in shape of the spathe pouch in the two species. Magnification about 90X.



